

# Spotted males, uniform females and the lowest chromosome number in Tettigoniids recorded: Review of the genus *Gonatoxia* Karsch (Orthoptera, Phaneropterinae)

Claudia Hemp<sup>1</sup>, Klaus-Gerhard Heller<sup>2</sup>, Elżbieta Warchałowska-Śliwa<sup>3</sup>, Andreas Hemp<sup>4</sup>

<sup>1</sup> Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, 60325 Frankfurt (Main), Germany

<sup>2</sup> Grillenstieg 18, 39120 Magdeburg, Germany

<sup>3</sup> Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland

<sup>4</sup> Department of Plant Systematics, University of Bayreuth, Germany

<http://zoobank.org/3F2DB40D-1E91-4061-9323-983DAC0D862B>

Corresponding author: Claudia Hemp (Claudia.Hemp@Senckenberg.de)

## Abstract

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The genus *Gonatoxia* Karsch, which was synonymized with *Dapanera* Karsch by Massa (2015), is re-established. Data on habitat, biology, ecology, the acoustics and on chromosomes are provided as well as a key to the species. The male of *G. immaculata* Karsch and the female of *G. maculata* Karsch are described. *G. furcata* sp. n. from the Udzungwa Mountains of Tanzania and *G. helleri* sp. n. inhabiting coastal and lowland wet forest are newly described. All species have calling songs consisting of very short, resonant syllables, produced in species specific intervals, and with peak carrier frequencies between 13 and 24 kHz. In respect to chromosome numbers *Gonatoxia* species showed extreme differences (from 29 to 7) suggesting rapid evolutionary changes. *G. helleri* sp. n. so far is the tettigoniid species with the lowest number of chromosomes at present. *Gonatoxia* species may be used as bioindicators, their presence suggesting valuable habitats that are vanishing rapidly in East Africa.

## Introduction

Lowland and coastal forests in East Africa are diminishing rapidly although their importance as hotspots of biodiversity and endemism are acknowledged (Burgess and Clarke 2000; Burgess et al. 2007). Coastal and lowland wet forests also harbor a high biodiversity of Orthoptera. Many Orthoptera species have a narrow ecological niche and are restricted to well defined plant assemblages (e.g. Hemp and Hemp 2003, Hemp 2005a, b) and can thus be used as bioindicators (Hemp et al. 2014), useful tools to

identify habitats deserving protection. The presence of e.g. *Tropidonotacris grandis* indicates dry deciduous forest or “Obstgartensteppe”, two habitat types highly endangered by habitat destruction in Tanzania (Hemp et al. 2014). The Phaneropterinae *Parapyrrhicia acutilobata* on the other hand indicates lowland wet forest, a forest type of which only few patches remained in East Africa (Hemp et al. 2016). If coastal forest is opened up or converted to grasslands the faunistic composition changes completely, mostly endemic and often flightless forest species are replaced by wide-spread and mainly fully mobile taxa (Hemp 2005b).

Until recently species of the genus *Gonatoxia* were poorly collected and little or no data were available on their biology, habitat or chromosomes. Karsch (1889) erected the genus *Gonatoxia* and described two species on two specimens, *G. immaculata* on a female from the Usambara Mountains, and *G. maculata* on a male from Somalia. In naming the species he referred to the maculae on the tegmina, present in the male of *G. maculata*, absent in the female *G. immaculata*. Very few specimens were collected of *G. maculata* since its description and stored in various entomological collections. For *G. maculata* a larger distribution area is suggested since the few known specimens were collected from Somalia, Kenya and Tanzania. For *G. immaculata* only the female holotype was known. When screening savanna habitats around Kilimanjaro at night larger numbers of *G. maculata* specimens could be collected in the past couple of years. When focusing on Tanzanian coastal and lowland wet forests specimens of *G. immaculata* were found. Only the study of a larger series of individuals clarified the status of the species which is now presented in this study. *G. furcata* sp. n. and *G. helleri* sp. n. are newly described and data on morphology, ecology, acoustics and chromosomes provided.

## Material and methods

**Measurements.** The total body length refers to the body length of the insect without tegmina. In females the ovipositor is not included in the body length, its length is taken from the tip to the base of the subgenital plate not considering the curvature. Length of tegmina are taken from above.

**Depositories.** NHML: British Museum, Natural History, London, U.K. MfN: Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin, Germany. ZMUC: Zoological Museum, Copenhagen, Denmark.

**Acoustics.** Songs were recorded in the laboratory using a digital bat detector (Pettersson D1000X) with sampling rates between 100 and 192 kHz and, additionally, a Sony ECM-121 microphone (frequency response relatively flat up to 30 kHz; own tests) connected to a personal computer through an external soundcard (Transit USB, "M-Audio"; 64-kHz sampling rate).

**Specimens recorded.** *Gonatoxia helleri* sp. n./Hemp 2016: Tanzania, Udzungwa Mts., 6 males (3 collected in the field, 3 reared from nymphs), Tanzania, Uluguru Mts., 4 males, Tanzania, Nilo forest reserve, 2 males. *Gonatoxia maculata* Karsch 1889: Tanzania, Mt. Kilimanjaro, 17 males (1 collected in the field, 16 reared from nymphs). *G. immaculata* Karsch, 1889 Tanzania, East Usambara Mountains, Sigi Trail, 1 male, Tanzania, Kisarawe, Kazimzumbwi Forest Reserve, 1 male. *G. furcata* sp. n. /Hemp 2016 holotype.

Song measurements and sonograms were obtained using AMADEUS II and AMADEUS Pro (Martin Hairer; <http://www.hairersoft.com>). Oscillograms of the songs

were prepared using TURBOLAB (Bressner Technology, Germany). All recordings were made at temperatures between 20 and 27 °C. The singers were caged in plastic tubes, wire mesh cages or gauze cages with microphone fixed or hand held at distances between 5 and 60 cm. Data are presented as mean ± standard deviation.

**Terminology.** Syllable: sound produced during one cycle of movements (opening and closing of the tegmina), in *Gonatoxia* equivalent to a pulse; echeme: first order assemblage of syllables; pulse: undivided train of sound waves increasing in amplitude at the beginning and containing many similarly sized wave maxima and minima (cricket-like song structure; example see Fig. 20).

**Chromosomes.** *G. maculata* (eleven males and one female), *G. immaculata* (two males and two females), *G. furcata* sp. n. (one male) and *G. helleri* sp. n. (twelve males and seven females) were used for classical cytotaxonomic analyses. Chromosome preparation was obtained from adult gonads and gastric caeca. Testes, ovaries and gastric caeca were excised, incubated in a hypotonic solution (0.9% sodium citrate), fixed in ethanol - acetic acid (3:1, v/v) and stored at 2 °C until use. The fixed material was squashed in 45% acetic acid. Cover slips were removed by the dry ice procedure and then preparations were air dried. Constitutive heterochromatin was revealed by the technique as described by Sumner (1972). Chromosomes were classified on the basis of the criteria proposed by Levan et al. (1964). At least ten spermatogonial and/or oogonial metaphase and/or 20 meiotic divisions (diakinesis and metaphase I) per male, were analyzed.

## Results

### Taxonomy

#### Genus *Gonatoxia* stat. rev.

Karsch, 1889 [1888]. Berlin Ent. Z. 32: 423, 441.

**Remarks.** Massa (2015) synonymized *Gonatoxia* with *Dapanera* since the males of *Dapanera* and *Gonatoxia maculata* have a similar outer appearance and genitalic morphology. Massa discussed that morphological differences between the genera *Dapanera* and *Gonatoxia* given by Karsch (1889) are too small to rectify genus status. Differences between the both genera referred to the fastigium of vertex not being sulcate in *Gonatoxia*, sulcate in *Dapanera*, the tegmina wider in *Gonatoxia* compared to *Dapanera* and the genicular lobes of the hind femora wearing a spine in *Gonatoxia* and are unarmed in *Dapanera*. Massa (2015) discussed that also *Gonatoxia* has a sulcate fastigium verticis and *Dapanera* species may have a small spine on the genicular lobes. The only distinguishing character between both genera remaining as given by Karsch (1889) was tegmina width.

Until recently little material was available in museum collections from the two known species of *Gonatoxia*. Now specimens of *G. maculata* were collected on Mt Kilimanjaro (Hemp 2013a), fair numbers of this species

few months later in savanna habitats and deciduous dry forests around Mt Kilimanjaro and in the North Pare Mountains (Hemp 2013b). Since many more specimens were collected now from various Tanzanian localities and compared to the types and each other it became clear that the females of *G. maculata* and *G. immaculata* are very similar and the majority of collected specimens were without maculae on the tegmina. Males of *G. maculata* as well as of *G. immaculata* have maculae on the tegmina, but clearly differing in their genitalic morphology. Thus the name given by Karsch (1889) referring to the maculae on the tegmina is misleading since in both species males have well developed maculae. A third species, *G. furcata* sp. n. was detected in the Udzungwa Mountains clearly separated from the other species by a different colour pattern and the male genitalic system. *G. helleri* sp. n. is very similar to *G. maculata* and intensive studies on its acoustics were conducted to separate these two species which occupy different habitats. The four species exhibit a very uniform outer morphology, the females having stout, little serrated and strongly up-curved ovipositors while all species of the genus *Dapanera* also uniformly have a more elongated ovipositor (Fig. 1) strongly differing in shape from that in *Gonatoxias*. All *Gonatoxias* species are stout with a vivid yellow dorsal abdomen (Fig. 2B). The male genitalia of *Gonatoxias* are only superficially similar to those of the genus *Dapanera*. Thus genus status is justified by a very homogenous outer morphology of *Gonatoxias* species (Fig. 2) compared to *Dapanera* species. Therefore it is proposed to reinstate the genus *Gonatoxias*.

### *Gonatoxias maculata* Karsch, 1889

Karsch. 1889[1888]. Berlin Ent. Z. 32:442.

**Material studied.** All Tanzania, 1 male, Mt Kilimanjaro, southern slopes, Msaranga valley, submontane riverine forest relicts, 1300 m, April 2011; 4 females, Mt Kilimanjaro, western slopes, Sanja Juu, 1300 m, savanna woodland May 2013; 3 males, 3 females, Mt Kilimanjaro, southern slopes, Rau forest near Moshi, lowland wet forest, 800 m, March, July, August, December 2014 and July 2015; 3 males, 4 females, North Pare Mountains, southern slopes, Lembeni, dry deciduous woodland, 1250 m, March, May, August 2013, May, November 2014 and July 2015; 1 female, Mt Kilimanjaro, southern slopes, Mabungu Hill, savanna woodland, 910 m, December 2013; 2 females, Mt Kilimanjaro, eastern slopes, Kirua, submontane savanna woodland 1300 m, July 2014; 1 female, Mt Kilimanjaro, eastern slopes, Holili, savanna woodland, 1300 m, June 2013 (collection C. Hemp).

**Further material studied.** 1 male, Somalia, Afgoi, Feb-March 1978, coll. A. Simonetta, B.M. 1979-543; 1 male, Kenya, Mombasa, coll. W. L. Slater, 1911-7. Depository NHML.

**Description. Male.** Males are characterized by a median deeply incised subgenital plate. The styli are long and slender and about 1.5 times longer than the medi-



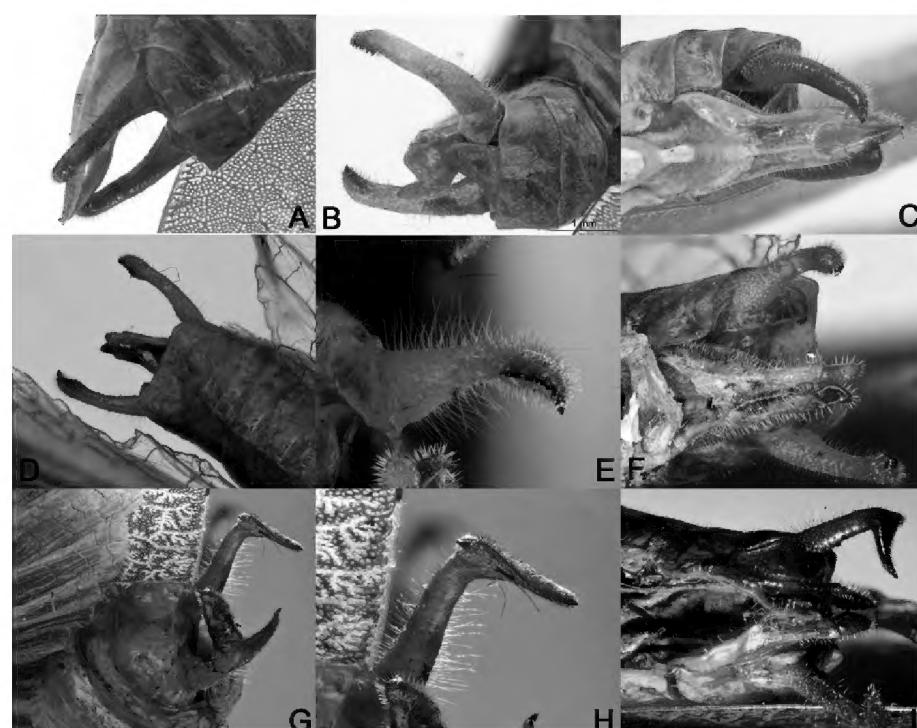
**Figure 1.** Lateral view on ovipositor of female *Dapanera* sp. Uganda (NHML).



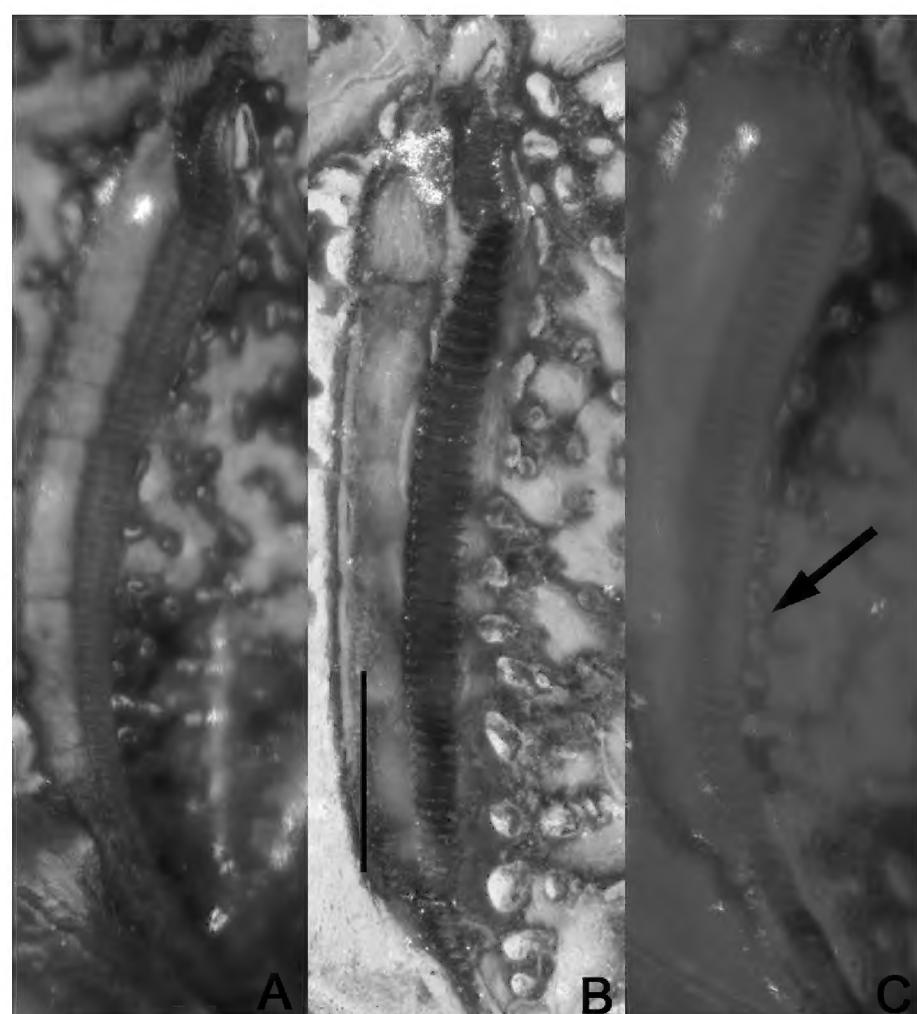
**Figure 2.** Habitus of *Gonatoxias* species. **A, B.** Male (A) and female (B) of *G. maculata*, Rau forest Kilimanjaro. Male with maculae on tegmina, female (B) showing the bright yellow tergites of abdomen, typical for all *Gonatoxias* species. **C.** Female *G. immaculata*, Kazimzumbwi Forest Reserve, Kisarawe near Dar es Salaam **D.** Female *G. furcata* sp. n., lowland forest Udzungwa Mountains, Morogoro District, Tanzania.

an incision (Fig. 3C). The cerci are stout, the tips wear a sclerotized ridge with numerous teeth (Fig. 3A, B). On the tegmina 2-6 white to ivory white patches are usually present which vary in number and size between the individuals (compare Fig. 2A). Teeth of stridulatory file at underside of left tegmen increase gradually in size (Fig. 4A) towards the anal end. Mirror area as in Fig. 5A, B.

**Female. General habitus and colour.** Predominantly green with broad oval tegmina and strongly up-curved ovipositor. Venation of tegmina often light green and often with tiny white dots scattered over tegmina, thus resembling a leaf perfectly. Whitish dots also on pronotum and legs. A pair of yellowish to whitish lines often present starting in upper part of compound eye and running over head and pronotum. Abdominal tergite bright yellow (2 B), tarsi whitish. **Head and antennae.** Antennae thin and whitish, surpassing tegmina. Eyes round, except for yellowish-whitish upper part green or brown-green. **Thorax.** Pronotal disc flat, longer posteriorly than pro-

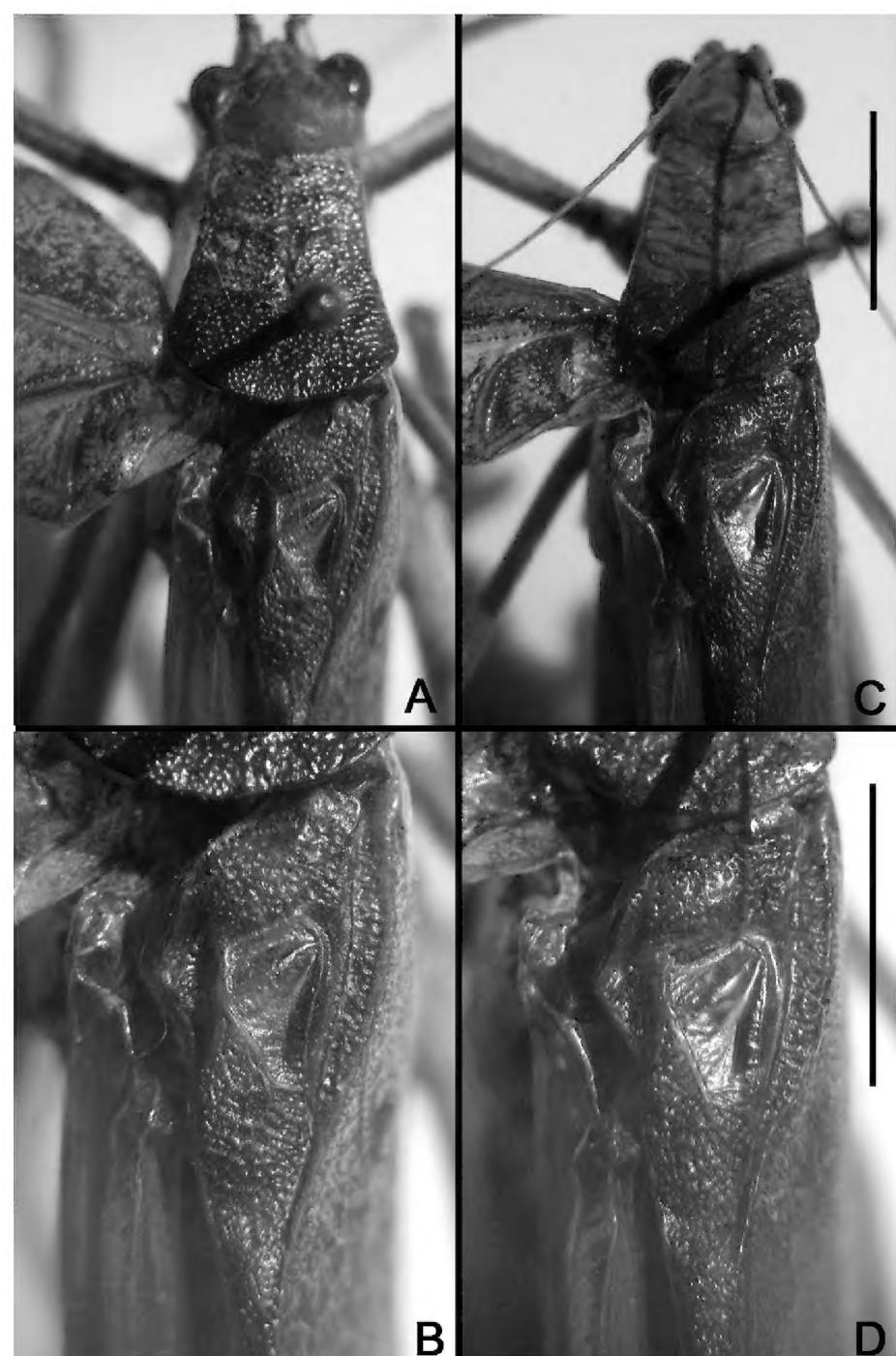


**Figure 3.** Morphological details of male *Gonatoxia* species. **A–C.** *G. maculata*, apex, semilateral view (A), dorsal view on cerci and apex (B), subgenital plate (C) **D–F.** *G. immaculata*, dorsal view on apex (D), right cercus (E), subgenital plate (F) **G–I.** *G. furcata* sp. n., semilateral view on apex (G), left cercus (H) and subgenital plate (I).



**Figure 4.** Stridulatory files of male *G. maculata* (A), *G. immaculata* (B) and *G. helleri* sp. n. (C). The arrow points to the discontinuity (elevation midway) typical for *G. helleri* sp. n. Scale bar 0.5 mm.

notal lobes which are evenly rounded at lower part, with acute edge at insertion of tegmina and wings. Tegmina broad with leaf-like pattern of veins, truncate at tips, alae surpassing tegmina. Alae hyaline except for tips which are of same green colour than tegmina. Stridulatory teeth on the right tegmen for female response to male calling song as in Fig. 6A. **Legs.** As in male. Fore femora with 3–4 outer spines, mid femora with 1–2 outer spines. Hind



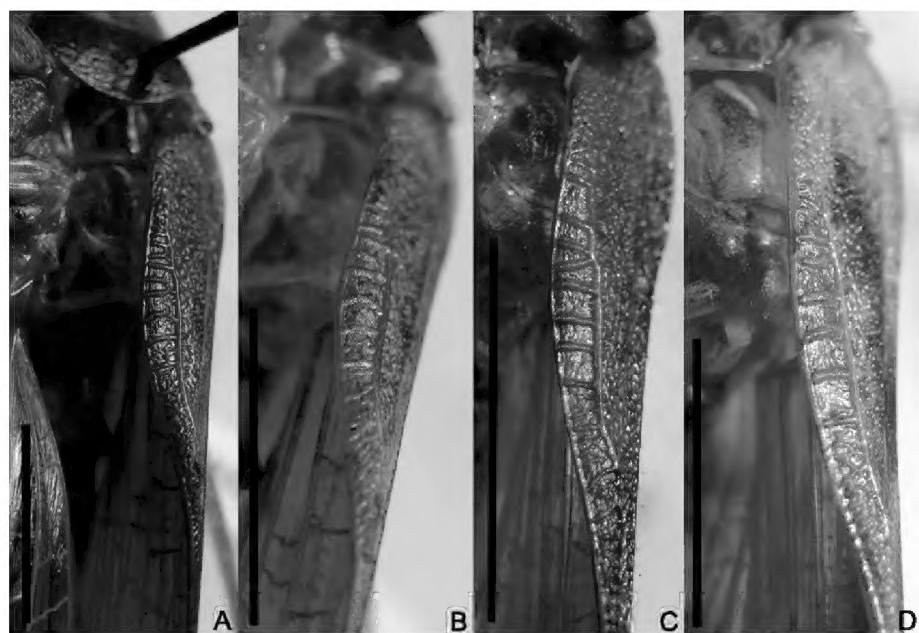
**Figure 5.** Pronotum and mirror area of male *G. maculata* (A, B) and male *G. helleri* sp. n. (C, D). Differences are small, the mirror of *G. helleri* sp. n. being more shiny and translucent. Scale bars 5 mm.

femora with 6–8 inner spines long whole length, outer side with 4–5 smaller spines at distal end of femur. Hind tibiae about length of hind femora, stout, in diameter almost tri-angular, curved. **Abdomen.** Plump abdomen with ovipositor strongly up-curved, valves at posterior third weakly sclerotized and serrated (Fig. 7A). Bowl-like structure lateral at base of ovipositor with strongly elevated lower margin, densely hairy in this region (Fig. 7A, 8A). Subgenital plate narrowly tri-angular (Fig. 9A). Cerci unmodified with stout base and slender elongated tip, strongly setose (Fig. 7A).

**Nymphs.** Nymphs similar to adults (Fig. 10A). When hatching recognized by curved hind tibiae (Fig. 11). Eggs are laid in rows glued to leaf tissue or along twigs (Fig. 12A, B).

**Measurements (mm).** **Females** (n = 5): Total length of body: 21.5–28.8; median length of pronotum: 6.1–6.3; length of hind femur: 26.2–27; length of tegmina: 41.8–44.7. Width of tegmina: 13.3–14.6; ovipositor: 5.3–5.8.

Since only data for the holotype male of *G. maculata* are available at present, we provide more measurement data.



**Figure 6.** Right tegmen with stridulatory veins of female *Gonatoxias* species **A.** *G. maculata* **B.** *G. immaculata* **C.** *G. helleri* sp. n. **D.** *G. furcata* sp. n. Scale bars 5 mm.

**Males** (n = 8): Total length of body: 23–28 (holotype 30); median length of pronotum: 6.1–6.6 (holotype: 7); length of hind femur: 25–27 (holotype 25); length of tegmina: 41–43.7 (holotype 41); width of tegmina: 10.3–14 (holotype 11.5).

**Biology.** A pair from Kilimanjaro mated on the 19<sup>th</sup> of November 2014. Mating only took a couple of minutes. A spermatophore containing a two-parted spermatophylax was transferred to the female (Fig. 13). Two days later the female laid 26 eggs into the tissue or on the margin of a broad leaf (Fig. 12A). When offered leaves and dried twigs, females usually laid eggs in series on twigs (Fig. 12B). First eggs from a further female (mating was not recorded) hatched on the 31<sup>st</sup> of July 2015 (Fig. 11) and the first adult moulted on the 11<sup>th</sup> of October 2015. Thus development of nymphs takes about 2.5 months (laboratory conditions).

In two matings (one male, two females; interval about two months) of culture-reared specimens the male weighed 1584 and 1590 mg and the females 1950 and 1830 mg (all before mating) and the two-parted spermatophores 214 and 169 mg (each value mean of male weight loss and female weight gain).

**Habitat.** Savanna woodlands and deciduous dry forest up to submontane elevations.

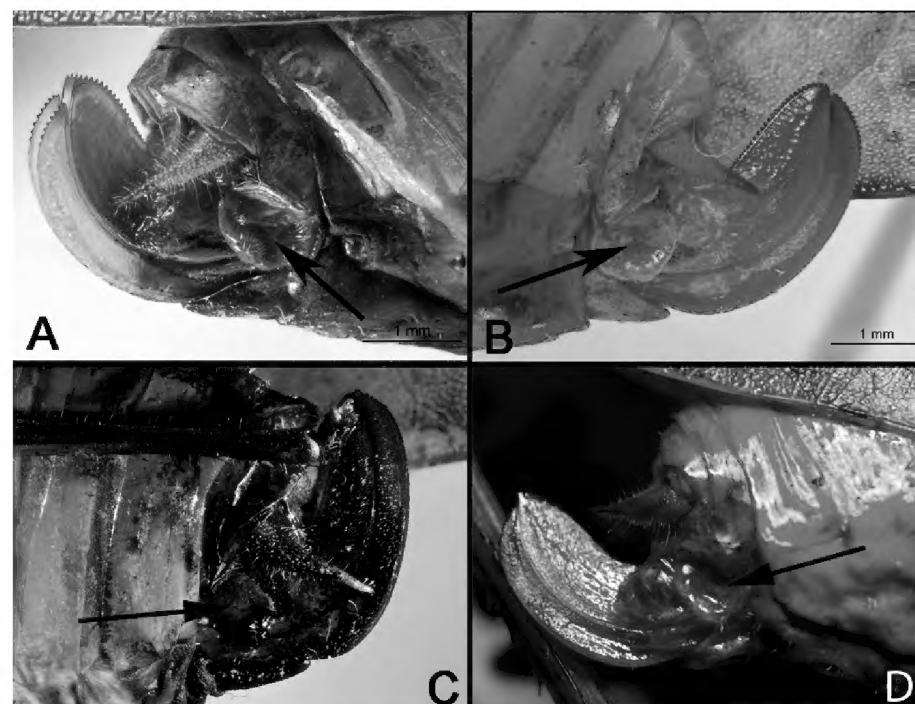
**Distribution.** Tanzania, Kenya, Somalia.

#### *Gonatoxias immaculata* Karsch, 1889

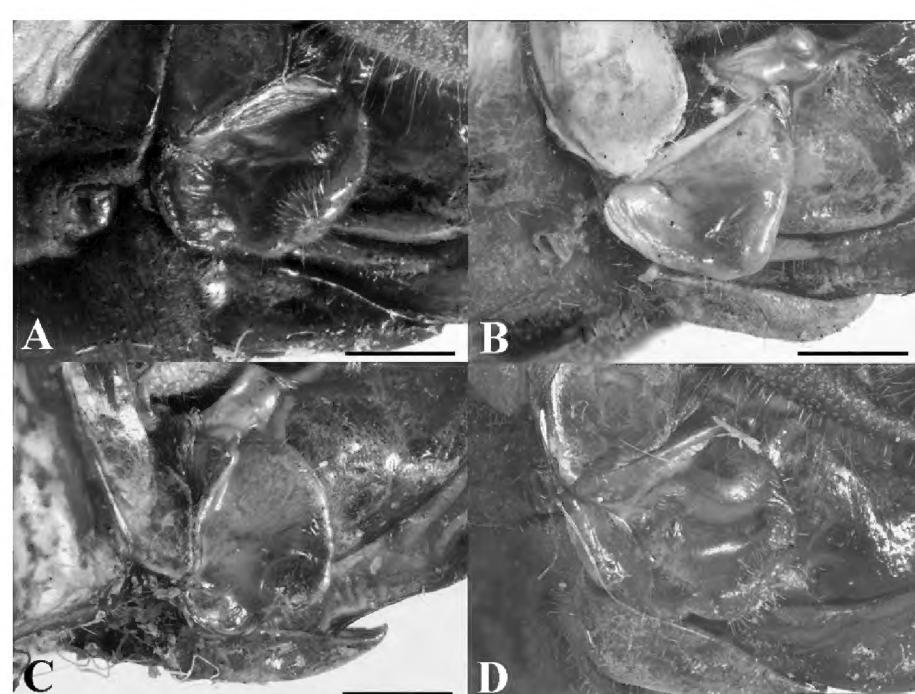
Karsch. 1889[1888]. Berlin Ent. Z. 32:442

**Material studied.** Female Holotype, Usambara, MfN.

**Further material studied.** Tanzania: 1 male, 4 females, Pwani Region, Kisarawe District, Kazimzumbwi Forest Reserve, 150 m, February and July 2015. 2 males, East Usambara Mountains, Nilo forest reserve, December 2015 and May 2016; 1 male, East Usambara Mountains, Sigi Trail, 450 m, lowland wet forest, November 2015 (Collection C. Hemp). 1 female, Kenya, Rabai, coll. A.F.J. Geydte Jan-Feb 1929 (NHML).



**Figure 7.** Lateral view on ovipositor of female *Gonatoxias* species. Note bowl-like structures laterally (arrows) **A.** *G. maculata* **B.** *G. immaculata* **C.** *G. furcata* sp. n. **D.** *G. helleri* sp. n. Scale bars 1 mm.



**Figure 8.** Bowl-like structures lateral at base of ovipositors of female *Gonatoxias* species. **A.** *G. maculata* **B.** *G. helleri* sp. n. **C.** *G. immaculata* **D.** *G. furcata* sp. n. Scale bars 1mm.

**Description. Male.** Color dark and shiny green, with few ivory to orange patches on tegmina; tergites of abdomen vivid yellow, venter whitish to light green; fore femora dorsally light brown, same colour as tarsi (Fig. 14). **Head and antennae.** Antennae thin, green, surpassing tegmina by about 1/3. Eyes round, brown-red. **Thorax.** Pronotal disc flat with sharp lateral edges, anterior margin v-shaped incurved, posterior margin of disc broadly rounded as described for genus (Karsch 1889). Lower margin of pronotal lobes broadly rounded, deeper than long, with sharp edge where wings are inserted. Tegmina broad, posterior end broadly truncate. Stridulation area tri-angle shaped flat on same level as pronotal disc as typical for genus. Stridulatory file as in Fig. 4B. Alae surpassing tegmina, in this area of same dark green shiny colour; with acute tips. Femora ventrally with spines. Fore tibiae slightly inflated in area of tympana. **Abdomen.** Last abdominal tergite with straight posterior margin (Fig. 3D). Cerci stout and setose; at tips

where serrated ridge starts slightly incurved (Fig. 3E), almost touching each other in alive insect. Subgenital plate with two short lobes, styli slightly inflated (Fig. 3F).

**Female.** Similar as male in habitus and colour. Stridulatory veins as in Fig. 6B. Ovipositor as in Fig. 7B. Bowl-like structure laterally on ovipositor more shallow as in *G. maculata* (Fig. 8C). Subgenital plate as in Fig. 9B.

**Nymphs.** Nymphs similar to adults (Fig. 10 B). Generally with a more shiny integument than in *G. maculata* (Fig. 10A) and with dorsal abdomen brown.

**Measurements** (mm). **Females** (n = 3): Total length of body: 23.8–25 (holotype: 27); median length of pronotum: 5.4–6.1 (holotype: 6); length of hind femur: 20–21.5 (holotype: 24); length of tegmina: 35.7–37.4 (holotype: 42). Width of tegmina: 12.1–12.6 (holotype: 14); ovipositor: 5–5.2 (holotype: 5).

**Males** (n = 2): Total length of body: 24–29; median length of pronotum: 6.2–6.7; length of hind femur: 21; length of tegmina: 36.2–42.3; width of tegmina: 11–13.5.

**Remarks.** When first males of *G. immaculata* were collected it became clear that specimens coming from Kazimzumbwi Forest Reserve belonged to *G. immaculata*. Thus the specimens from the spirit collection of the Zoological Museum Copenhagen listed as *G. maculata* from Kazimzumbwi Forest Reserve in Hemp (2013b) belong to *G. immaculata*.

**Habitat.** Lowland wet forest to submontane wet forest.

**Distribution.** Coastal Tanzania, East and West Usambara Mountains.

#### *Gonatoxia furcata* C. Hemp, sp. n.

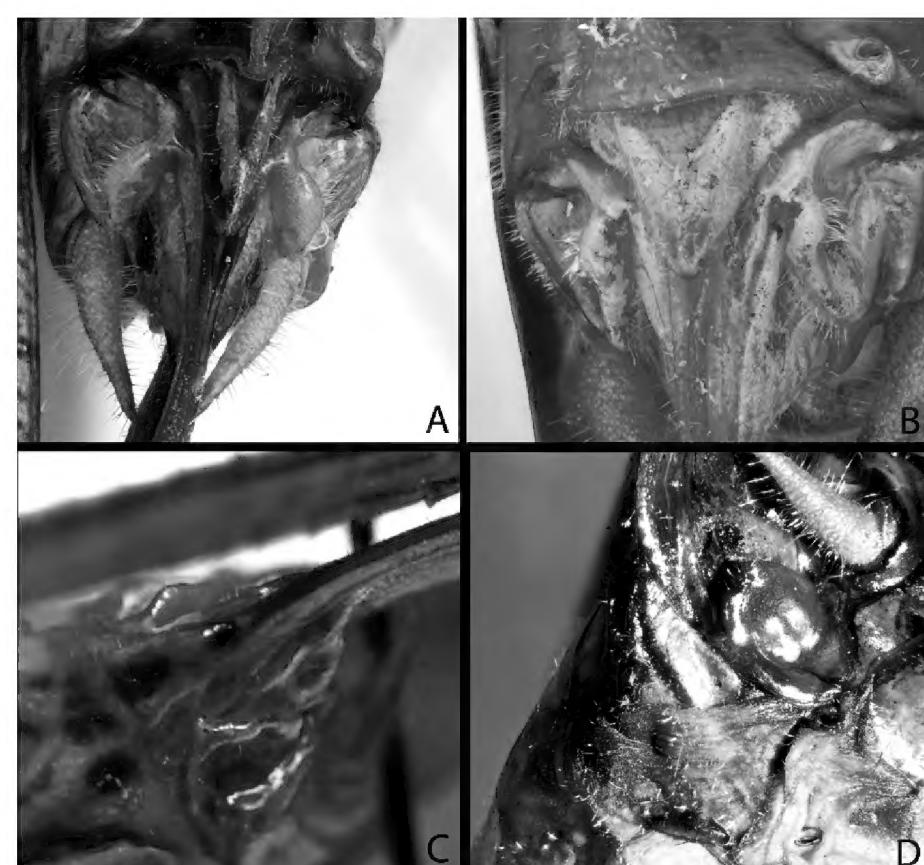
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**Holotype male.** Tanzania, Morogoro District, Udzungwa Mountains, National Park Headquarters, Mangula Gate, 300 m, lowland wet forest, July 2015. Depository MfN.

Paratype female, same data as holotype but March 2015. Depository MfN.

**Further paratype material.** 3 females, same data as holotype, May and June 2016 (collection C Hemp). 1 male (in alcohol), Tanzania, Iringa Region, Mufindi District, Udzungwa Scarp Forest Reserve, 08°31.5'S 35°53.9'E, 750 m, March 1996, McKamey et al. leg., depository ZMUC.

**Diagnosis.** Females of *G. maculata*, *G. immaculata* and *G. furcata* sp. n. are very similar. Differences are seen in the general coloration especially when specimens are alive. *G. maculata* and *G. helleri* sp. n. females are of lighter green colour while those of *G. immaculata* and especially *G. furcata* sp. n. are darker green and the tegmina shiny (Fig. 2B, C, D). The subgenital plate in *G. maculata* is not as broad as those of *G. helleri* sp. n., *G. immaculata* and *G. furcata* sp. n. (Fig. 9A, B, C, D) but the differences are not very pronounced. Lateral at the base of the ovipositors a bowl-like structure is present in all *Gonatoxia* species (arrows Fig. 7). In *G. maculata* this bowl-



**Figure 9.** Subgenital plates of female *Gonatoxia* species. **A.** *G. maculata* **B.** *G. immaculata* **C.** *G. helleri* sp. n. **D.** *G. furcata* sp. n.

like structure is large and more deeply excavated than in *G. immaculata* (Fig. 8A). In *G. furcata* sp. n. inside the “bowl” a hump is located at the upper part and the lower margin is not hairy as in the other two species. The bowl-like structure in *G. helleri* sp. n. is very shallow and not as setose (Fig. 8B). Further *G. immaculata* females are smaller than those of *G. maculata* and *G. helleri* sp. n. while *G. furcata* sp. n. females are generally larger than those of the other three species.

Males are distinguished when comparing the outer genitalic morphology. In *G. maculata* the cerci are evenly tapering to their apices, the tips wearing a short and straight serrated ridge (Fig. 3B) while in *G. immaculata* the tips of the cerci wear a longer and curved serrated ridge (Fig. 3D, E). *G. helleri* sp. n. has similar built cerci as *G. maculata* but instead of a serrated ridge (Fig. 3B) a smaller ridge or 1–4 closely clustered teeth are located at the tips. In *G. furcata* sp. n. the tips of the male cerci are elongated, scythe-shaped with a very long serrated ridge (Fig. 3G, H, I). Males of all four species have maculae on the tegmina (Fig. 15). In *G. maculata* these white patches can be small or large and conspicuous, most specimens had 3–6 of these markings. In the known specimens of *G. immaculata* the patches were orange-brown (Fig. 14, 15C). The maculae of *G. furcata* sp. n. resemble those of *G. immaculata*, being orange-brown. *G. helleri* sp. n. usually has small longish white maculae and mostly not more than 2–4 (Fig. 15B, 16A).

**Description. Male.** Color dark and shiny green, with few ivory patches on tegmina; tergites of abdomen vivid yellow, venter whitish to light green; fore femora dorsally light brown, same colour as tarsi, thus similar to *G. immaculata*. **Head and antennae.** Antennae thin, green, surpassing tegmina by about 1/3. Eyes round, green, with light stripe beginning in eyes, running over the head getting yellow along lateral edges of the pro-



**Figure 10.** *Gonatoxia* nymphs. **A.** *G. maculata*, last instar **B.** *G. immaculata* 4th instar.



**Figure 11.** Hatching nymph of *G. maculata*.

notum. *Thorax*. Pronotal disc flat with sharp lateral edges, anterior margin v-shaped incurved, posterior margin of disc broadly rounded as described for genus (Karsch 1889). Lower margin of pronotal lobes broadly rounded, deeper than long, with sharp edge where wings are inserted. Tegmina broad, posterior end broadly truncate. Stridulation area tri-angle shaped flat on same level as pronotal disc. Stridulatory file evenly tapering in dent size. Alae surpassing tegmina, in this area of same dark green shiny colour; with acute tips. Femora ventral-

ly with spines. Fore tibiae slightly inflated in area of tympana. *Abdomen*. Last abdominal tergite with straight posterior margin (Fig. 3G). Cerci stout and setose; tips scythe-shaped with long serrated ridge (Fig. 3G, H, I). Subgenital plate with very short lobes, styli slightly inflated (Fig. 3I).

**Female.** Similar as male in habitus and colour (Fig. 2D) but with broader tegmina. Stridulatory veins as in Fig. 6D. Ovipositor as in Fig. 7C, subgenital plate as in Fig. 9C.



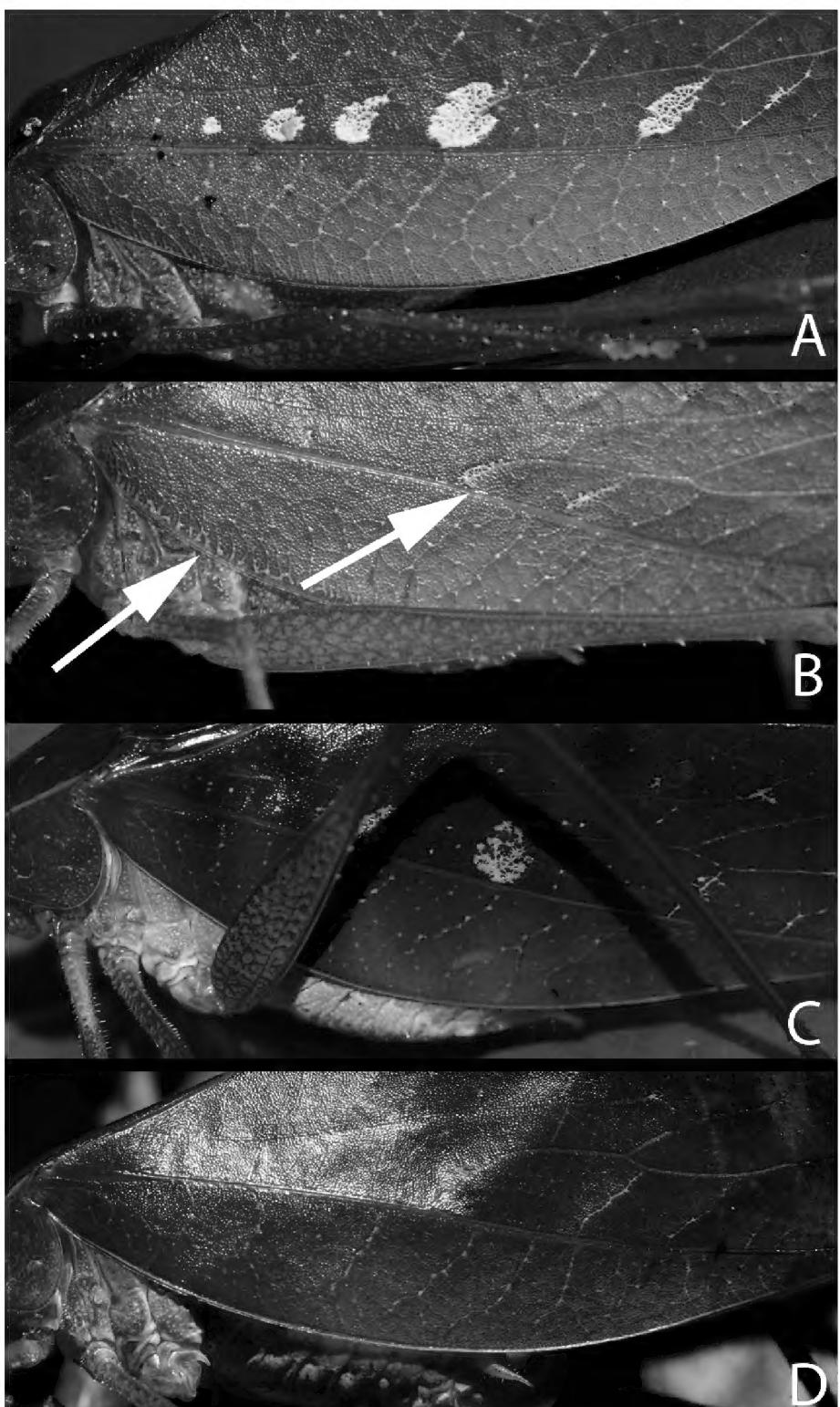
**Figure 12.** Freshly laid eggs of *Gonatoxia maculata* (A). 26 eggs were laid two days after mating and hatched 7 months later. (B) Eggs glued on a twig.



**Figure 13.** Pair of *Gonatoxia maculata* shortly after mating. Note the white spermatophore at the abdomen of the female.



**Figure 14.** *Gonatoxia immaculata* male, East Usambara Mountains. Note the orange patches on the tegmina and the deep green shiny colour.



**Figure 15.** Left wings of male *G. maculata* (A), *G. helleri* sp. n. (B), *G. immaculata* (C) and female *G. furcata* sp. n. (D). Morphological differences between *G. maculata* and *G. helleri* sp. n. are small. However, usually *G. maculata* (A) have more and larger maculae on the tegmina while *G. helleri* sp. n. (B) have fewer maculae that are smaller and longish and usually start where *Rs* branches off (right arrow). Also *G. helleri* sp. n. has a white bordered costal margin with veins branching off white and thickened (left arrow).

**Measurements (mm).** **Females** (n=3). Total length of body: 26–27; median length of pronotum: 6.3–6.5; length of hind femur: 25–26.6; length of tegmina: 48–49; width of tegmina: 16; ovipositor: 5.5–6.

**Males** (n=1): Total length of body: 31.5; median length of pronotum: 6.9; length of hind femur: 25; length of tegmina: 43. Width of tegmina: 13.4.

**Etymology.** from Latin: *furca* = fork because of the forked male cerci.

**Habitat.** Lowland wet forest.

**Distribution.** At present only known from the Udzungwa Mountains, Tanzania.

**Gonatoxia helleri C. Hemp, sp. n.**

<http://zoobank.org/9BA1D6AD-AA58-4706-B93C-CF9FC2D94438>

**Holotype male.** Tanzania, Uluguru Mountains, Morogoro District, forest above Morningside, February 2016. Depository MfN.

Paratype female, same data as holotype; depository MfN.

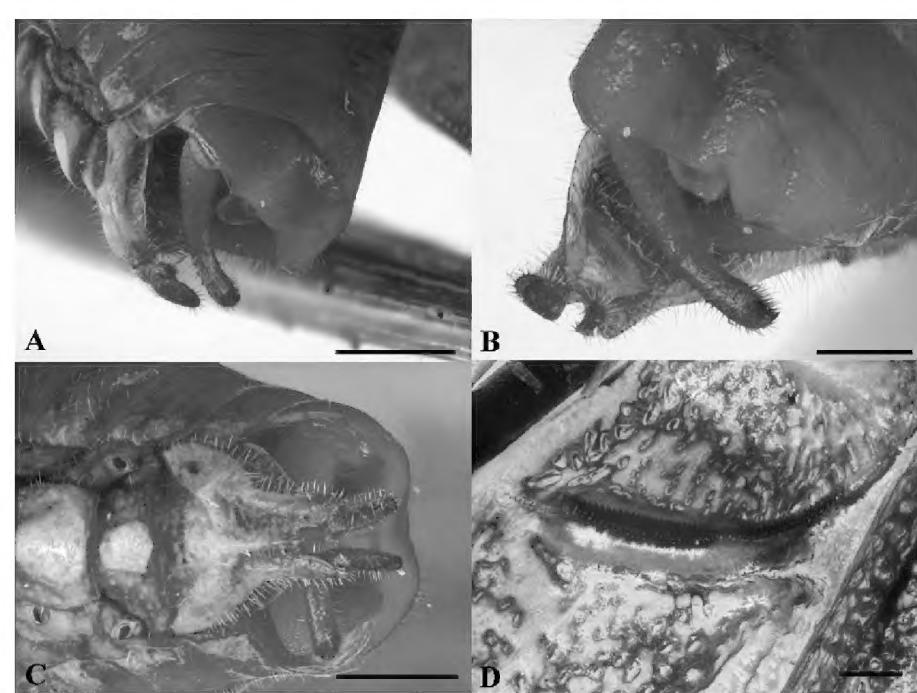
**Further paratypes.** All Tanzania; 13 males, 17 females, same data as holotype, March and April 2016; 3 males, 1 female, East Usambara Mountains, Nilo forest reserve, February and May 2016; 1 male, East Usambara Mountains, Sigi Trail, lowland wet forest, 450 m, November 2015; 1 male, 4 females, West Usambara Mountains, Lutindi Mental Hospital, submontane forest, 1250 m, February 2015 and June 2016; 1 male, 1 female, West Usambara Mountains, Mazumbai forest reserve, 1600 m, March 2016; 7 males, 3 females, Udzungwa Mountains National Park, Mangula Gate, lowland wet forest, 300 m, March, July, September 2015, January, March and May 2016; 1 female, Kisarawe District, Kazimzumbwi Forest Reserve, February 2015 (collection C. Hemp).

**Further material studied.** 1 male, Kenya?, Kibatuga, 20/10/51, B.M 1966–628; 1 female, East Africa 82/24, Tanzania, Korogwe-Msata Road, 103 km north of Msata, summit of kopj, 21 IX 1982, coll. N. Jago; 1 female, Tanzania, Kilosa. 10 IX 1926, coll. N. C. E. Miller, B.M. 1928–281; 1 female, Tanzania 63, B.M. 1950–96; 1 female, Tanzania, Lindi, Ndanda, 300 m, 5. III 1952, coll. Lindemann and Pavlitzki; 1 male, N Derema, coll. G. v. Son, B.M. 1969–331 (depository: NHML). The specimens from the collection of the NHML are not listed as paratypes since they were either females that are difficult to identify without males or males where the stridulatory file could not be studied.

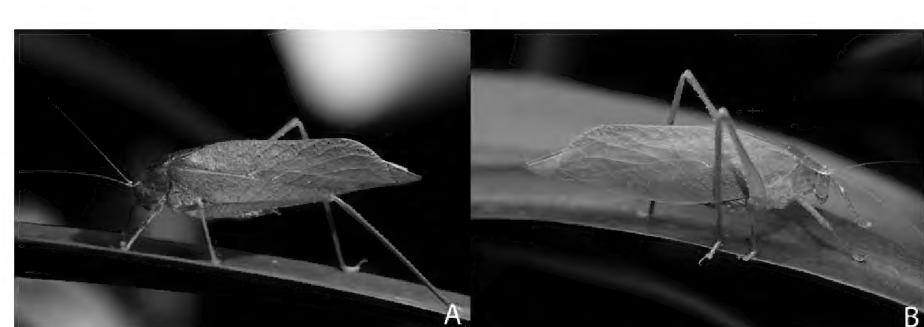
**Diagnosis.** *G. helleri* sp. n. is very similar to *G. maculata*. Both species have about the same size and colour and shape of tegmina and wings. However, *G. helleri* sp. n. usually have far less conspicuous maculae on the tegmina, being smaller and more longish and fewer in number. Mostly these maculae start about where the Rs vein branches off. Typical is also a dense net of white veins, especially in the costal area of the tegmen forming multiple small white dots. Also the costal margin is bordered white with veins branching off thick and very white in both sexes when alive (weakly expressed in the Udzungwa population of *G. helleri* sp. n.). The males of *G.*

*helleri* sp. n. can also be distinguished from *G. maculata* by in the male cerci wearing a smaller sclerotized ridge or 1–4 single teeth clustered tightly together whereas *G. maculata* males wear a stouter and larger serrated ridge at the tips of the male cerci. Differences are also seen in the stridulatory file of the males. The stridulatory file of *G. maculata* evenly tapers in dent size from one side to the other (Fig. 4A) while in *G. helleri* sp. n. the stridulatory file is somewhat constricted and elevated midway with larger teeth following running to the margin of the left tegmen (Fig. 18; Fig. 4C, arrow) and thus dividing the whole structure into three parts. *G. helleri* sp. n. has a male subgenital plate which is not as deeply incised as in *G. maculata* and the styli are flattened and broad (Fig. 17C) while in *G. maculata* the subgenital plate is deeper incised and the cerci longer and more stout (Fig. 3C). *G. immaculata* and *G. furcata* sp. n. both are shiny dark green usually, *G. immaculata* males often have conspicuous white to orange patches on the tegmina. The cerci of male *G. immaculata* have a sclerotized curved ridge at their tips while *G. furcata* sp. n. males have scythe-shaped cerci. The females are often difficult to identify since also more light green individuals of *G. immaculata* occur and the shiny colour vanishes in preserved specimens. Further *G. helleri* sp. n. was found syntopically with *G. immaculata* in the East Usambara Mountains. In the Udzungwa Mountains *G. helleri* sp. n. occurs syntopically with *G. furcata* sp. n. However, *G. furcata* sp. n. females are generally larger than *G. helleri* sp. n. females and of shiny dark green colour. *G. immaculata* females are difficult to distinguish from *G. helleri* sp. n. females and only the study of larger series comparing the bowl-like structure laterally on the ovipositor may help to identify females of both species, especially in preserved specimens.

**Description. Male.** *General habitus and colour.* Predominantly green with oval tegmina and 2–4 small ivory



**Figure 17.** Morphological details of male *Gonatoxia helleri* sp. n. **A.** Semilateral view on abdominal apex. Scale bar 1 mm **B.** Dorsal view on abdominal apex with sclerotized ridge of cercus. Scale bar 1 mm **C.** Subgenital plate. Scale bar 1 mm **D.** Stridulatory file. Scale bar 500 µm.



**Figure 16.** *G. helleri* sp. n., male (A) and female (B) from the Uluguru Mountains.

patches on tegmina (Fig. 16A). Whitish dots also on pronotum and legs. Pair of white lines often present starting in upper part of compound eye and running over head and pronotum. As in all *Gonatoxia* species abdominal tergite bright yellow, tarsi whitish. *Head and antennae*. Antennae thin and whitish, surpassing tegmina. Eyes round, except for whitish upper part green or light green. *Thorax and wings*. Pronotal disc flat, longer posteriorly than pronotal lobes which are evenly rounded at lower part, with acute edge at insertion of tegmina and wings. Tegmina broad with leaf-like pattern of the veins, slightly truncate at tips, alae surpassing tegmina. Alae hyaline except for tips which are of same green colour than tegmina. Tegmina with net of white veins, on veins often white dots are formed, especially in costal area (Fig. 15B). Costal margin white bordered with veins directly branching off at margin thick and white. Stridulatory file (Fig. 17D) separated into three parts with small teeth near tegmen base, an elevation midway (arrow Fig. 4C) and large teeth at outer part of file. *Legs*. Fore femora with one outer spine and 1–4 inner spines ventrally. Mid femora with 3 outer and no inner ventral spines. Hind femora with double row of irregular set of 7–8 ventral spines. Fore tibiae in area of tympana slightly enlarged, with conchate inner tympanum and open oval tympanum on outer side; midway dorsal one spine, ventral several irregular set spinules. Mid tibiae with irregular set spinules in four rows. Hind tibiae dorsally two ridges densely covered by small spines, ventral side with few

irregular set spines, curved. *Abdomen*. Venter white. Cerci slender and incurved (Fig. 17A, B), at tips with short ridge or 1–4 single sclerotized dents. Subgenital plate medially u-shaped incised, styli flat, roundish and somewhat inflated, touching each other medially when insect is alive (Fig. 17C).

**Female.** Similar to male in size but with more roundish tegmina and mostly without ivory patches on tegmina or 1–2 and very small ones, mostly where Rs branches off. Also with for this species typical costal margin bordered white with branching off veins thicker and white and net of white veins forming white dots. Stridulatory veins as in Fig. 6C. Ovipositor up-curved, serrated at tip (Fig. 7D). Bowl-like structure formed laterally on base of ovipositor as in Fig. 8B. Subgenital plate tri-angular (Fig. 9C).

**Body mass.** (mg; n=1) Male 990. Female 1462 (culture-reared, 01.08.2015).

**Measurements (mm).** **Females** (n=6): Total length of body: 25.8–27.5; median length of pronotum: 6.5–6.8; length of hind femur: 26.5–28.6; length of tegmina: 44.0–45.9; width of tegmina: 14.8–14.4; ovipositor: 5.2–5.4.

**Males** (n=6): Total length of body: 23.5–26.4; median length of pronotum: 5.7–6.5; length of hind femur: 25–28; length of tegmina: 42.5–44.4; width of tegmina: 12.5–13.4.

**Etymology.** Named after Klaus-Gerhard Heller.

**Habitat.** Lowland wet to submontane forest.

**Distribution.** Tanzania and very likely Kenya.

### Key to males of *Gonatoxia*

1	Male cerci not scythe-shaped .....	2
–	Male cerci scythe-shaped (Fig. 3G, H).....	<i>G. furcata</i> sp. n.
2	Male subgenital plate deeply medially incised, styli long and slender, about 1.5 times as long as incision (Fig. 3C) .....	<i>G. maculata</i>
–	Male subgenital plate not deeply medially incised, styli not longer than incision, broader and compressed.....	3
3	Cerci with short straight sclerotized ridge at tips (Fig. 17B); subgenital plate u-shaped incised forming stout lateral processes and oval slightly compressed styli (Fig. 17C) .....	<i>G. helleri</i> sp. n.
–	Apices of male cerci inwardly curved and with long sclerotized serrated ridge (Fig. 3 E) .....	<i>G. immaculata</i>

### Bioacoustics

**Morphology of stridulatory organs:** In the male, the slightly curved stridulatory file (Fig. 4) is found on the underside of the left tegmen, carrying between 50 and 60 teeth. On the corresponding place of the right tegmen there is a similar sized (non-functional) file. At the anal end there is no trace of a lump or comparable structure. On the contrary, the file starts with a few weakly sclerotized teeth, which lead up to the elevated main part of the file. Here the steep side of the teeth is directed towards the anal end (Fig. 18; see Discussion). The inter-tooth intervals in *G. maculata* (n=2), *G. immaculata* (n=2) and *G. furcata* sp. n. (Holotype) decrease more or less continuously from 50 µm at anal end to 30 µm near the articulation (Fig. 19). In *G. helleri* sp. n. however, there is a discontinuity

in the middle (see arrow in Fig. 4C), and the intervals in the basal part are around 55 µm (n=3). For function of this file part see Heller and Hemp, in prep. The mirror is relatively small and inconspicuous (Fig. 5), in *G. helleri* sp. n. a little bit more glossy than in *G. maculata*.

The females bear one distinct row of spines on each of several veins on the upper side of the right tegmen (Fig. 6; about eight in *G. maculata*) as it is typical for acoustically responding phaneropterine females (Heller et al. 2015).

**Spectral composition of song:** The frequency spectra of the male songs were relatively narrow-banded in all four species studied (for example see Fig. 20). In *G. maculata* the peak is between 12.6 and 17.4 kHz (n=17), in *G. immaculata* between 17.0 and 23.6 kHz (n=2), in *G. fur-*

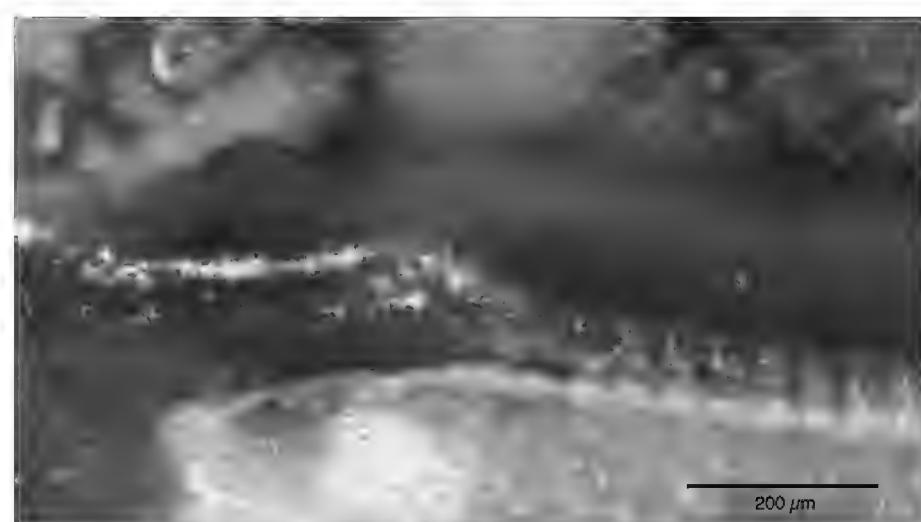
*cata* sp. n. 16.9 kHz (n=1) and in *G. helleri* sp. n. between 15.6 and 20.8 kHz (n=7). The bandwidth 10 dB below the peak was always between 1.3 and 3.9 kHz. All data refer to the first syllable of a pair of syllables (see below).

**Song pattern.** The calling songs of all studied species consisted of short (1–4 ms), resonant syllables (Fig. 21), often emitted in pairs. Comparing the grouping of these syllables or syllable pairs, the species can be separated into two groups. The first group consists of *G. maculata* and *G. helleri* sp. n. Isolated physically and acoustically, the males of these species produced long sequences of pulses. These series typically lasted 30 to 90 seconds and were separated by intervals of many minutes. Within a sequence, *Gonatoxia maculata* nearly always emitted pairs of pulses with intra pair intervals of about 70 ms and inter pair intervals of 2 s. In the song of *G. helleri* sp. n. pairs of pulses and single pulses were found, with intra pair

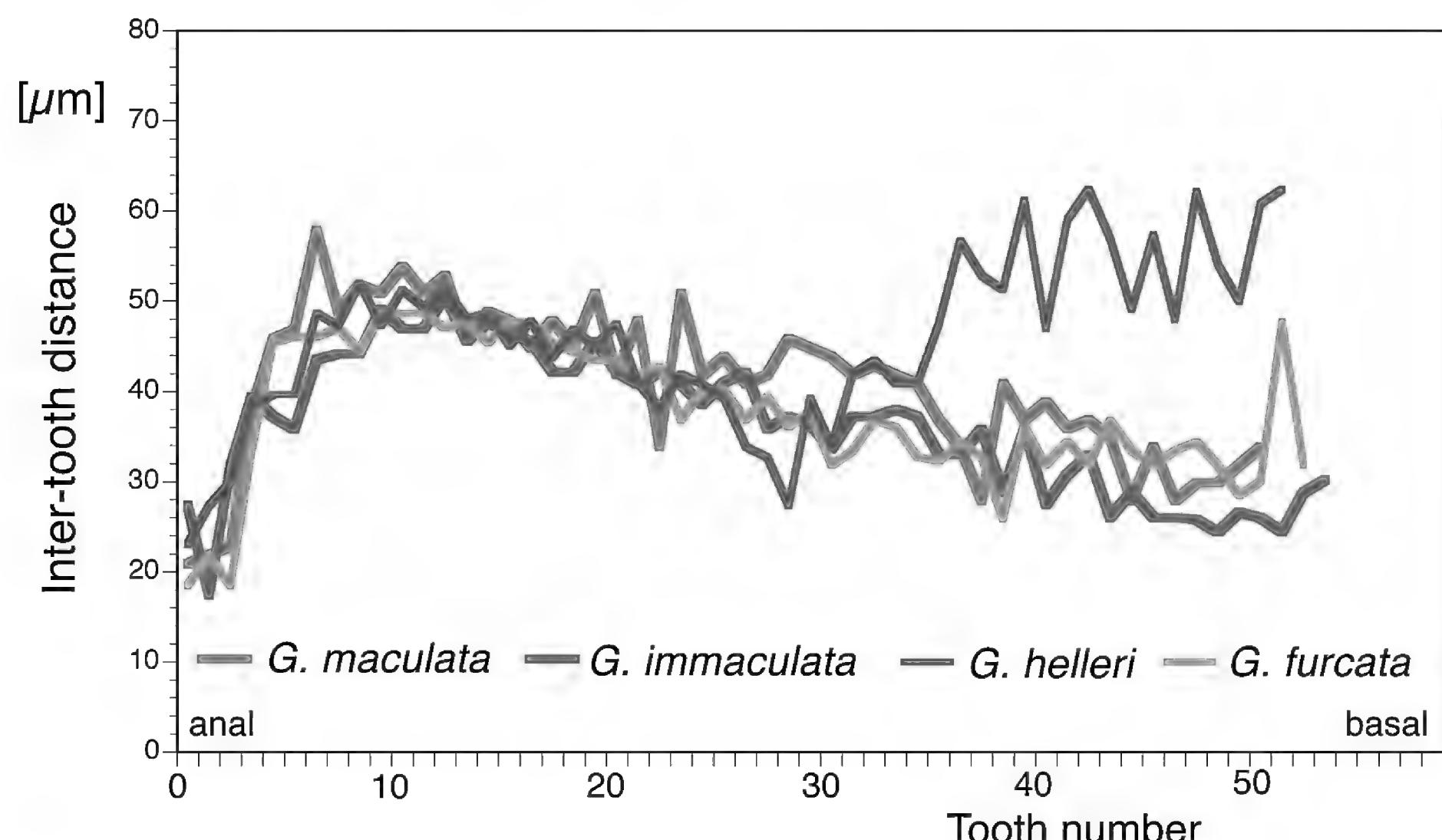
intervals as in *G. maculata* and intervals between pairs/single syllables ca. 0.3–1 s. Additionally, in many recordings of both species stereotypic combinations of pulses were found, where an additional pulse (or a very dense pulse group) following after a pair (or in *G. helleri* sp. n. sometimes a single pulse) in an interval of about 250 ms. These combinations belong to the acoustical male-female-interactions and will be treated in a separate paper (Heller and Hemp, in prep). The males of the second group, consisting of *G. immaculata* and *G. furcata* sp. n., produced much shorter syllable series, lasting only a few seconds, and the intervals between the syllable pairs were also much shorter than in the first group. In *G. immaculata* the intra-pair interval was about the same as in the song of the members of the first group. However, both recorded males showed distinct differences concerning the inter-pair intervals and the frequency of single pulses. In *G. furcata* sp. n., the intra-pair interval was with about 120 ms distinctly larger than in the other three species. In this species, some of the short series followed each in relatively short intervals.

### Cytotaxonomy

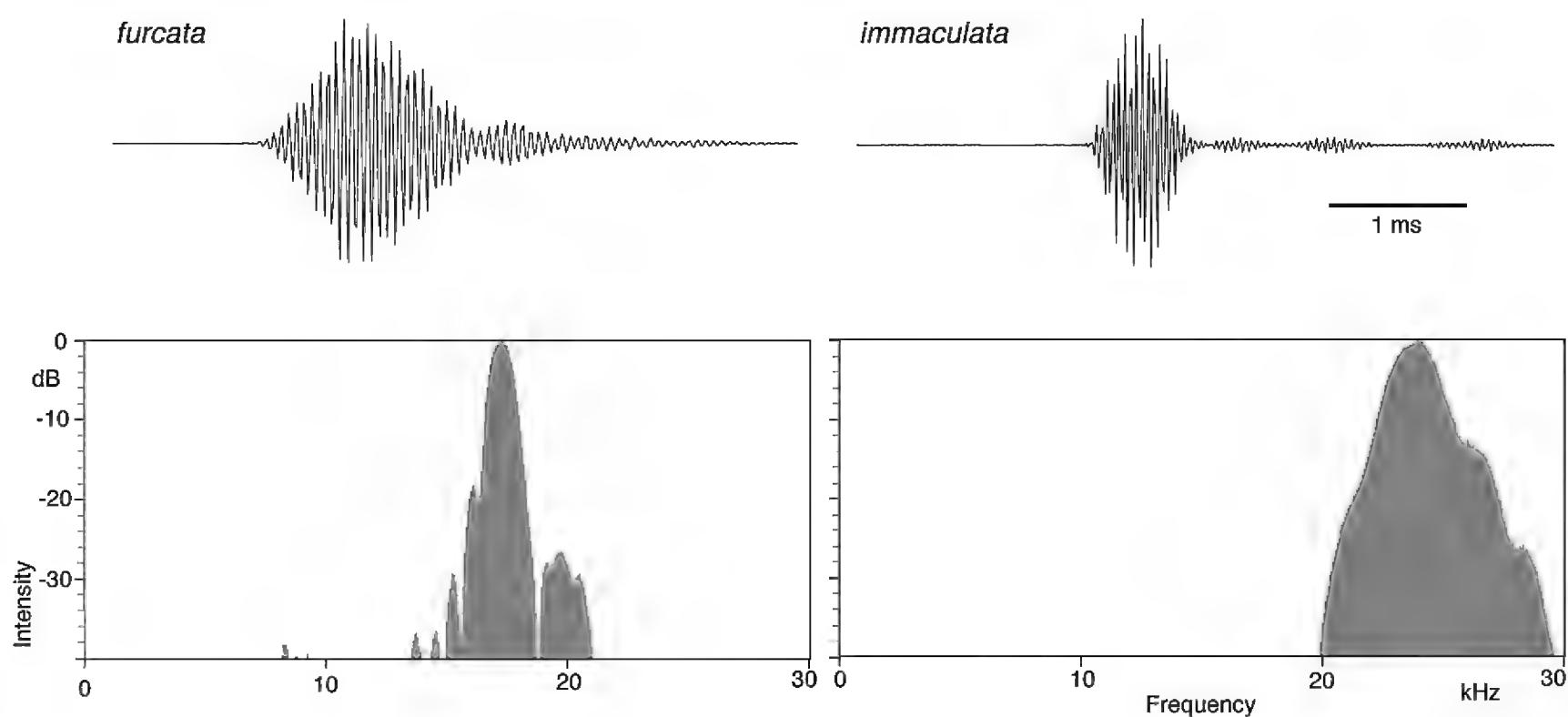
Comparison of the chromosomes of four *Gonatoxia* species revealed differences between their karyotypes, including the number of chromosomes (2n), the morphology of the chromosomes, the fundamental number of chromosome arms (FN) and C-banding patterns. All analyzed species show the same sex determining system: X0 (male) and XX (female) as well as the acrocentric X chromosome which is the largest element of the set.



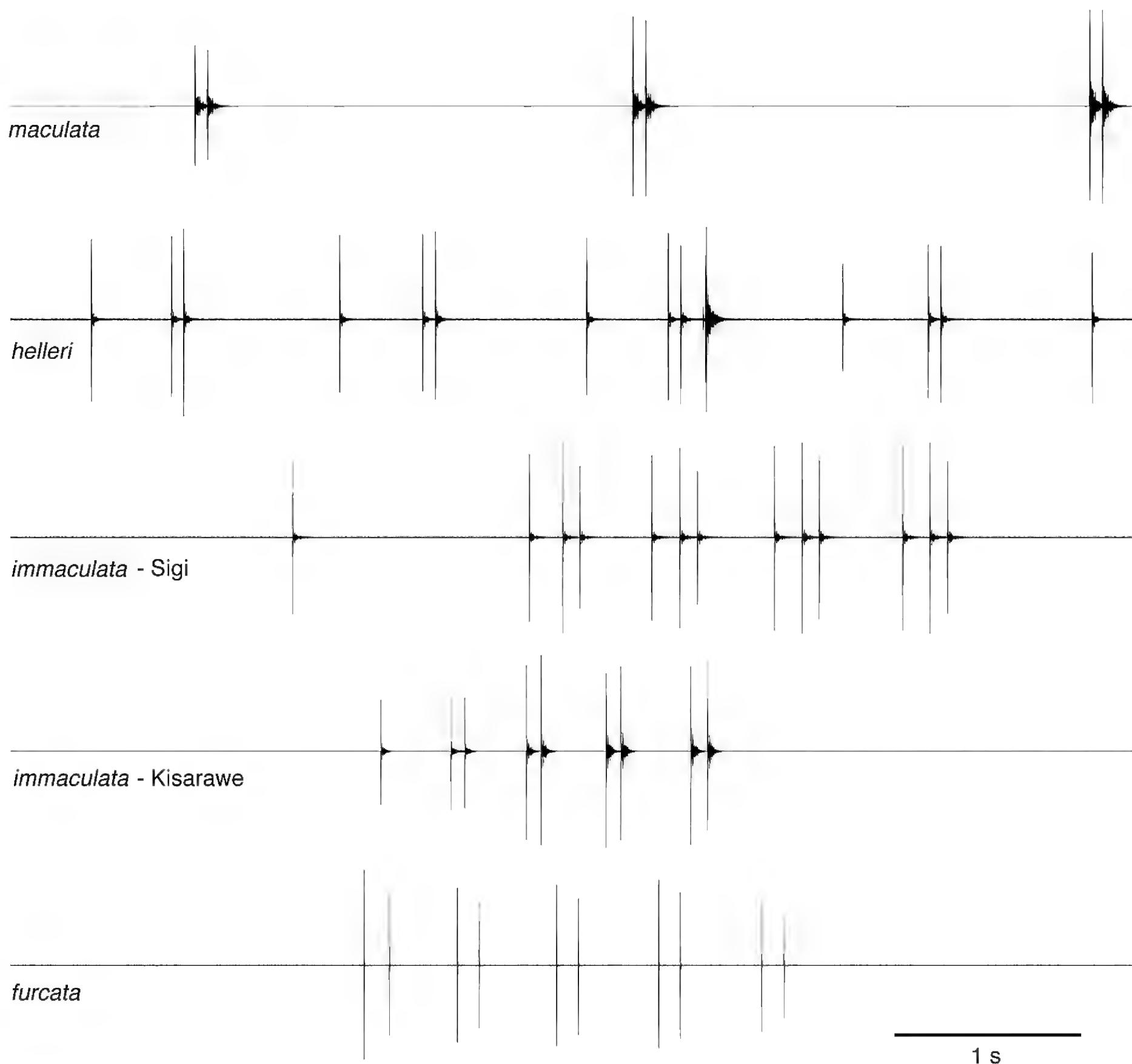
**Figure 18.** Detail of stridulatory file of *Gonatoxia immaculata* with teeth directed towards the anal end.



**Figure 19.** Inter-tooth spacing in stridulatory files of male *Gonatoxia* species (most intervals between small teeth at the anal end not measured).



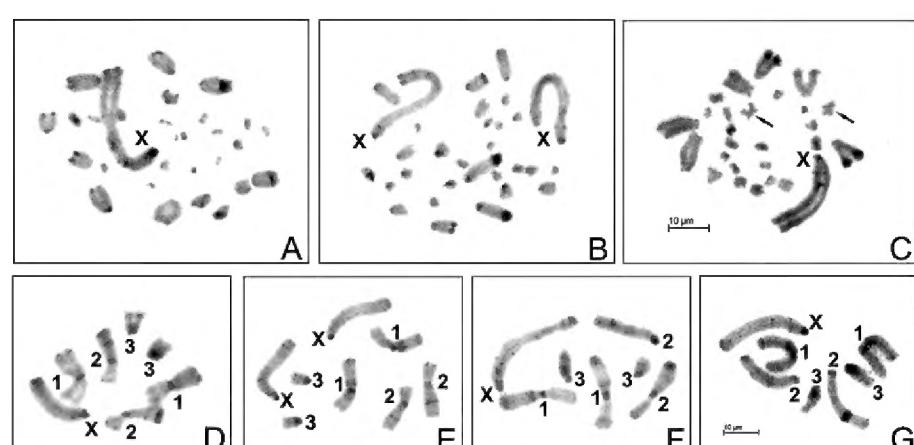
**Figure 20.** Oscillograms of single syllables of the male calling song and corresponding spectral composition (power spectra).



**Figure 21.** Oscillograms of the male calling song of *Gonatoxia* species. In *G. maculata* and *G. helleri* only part of a much longer sequence is shown, in *G. immaculata* and *G. furcata* complete series.

The standard karyotypes of *G. maculata* and *G. immaculata* were characterized by a chromosome number of  $2n = 29$  (males) and 30 (females). All chromosomes were acrocentric, consisting of three long, four medium and seven short pairs (Fig. 22A, B). In the single male investigated of *G. furcata* sp. n. (Fig. 22C) and one male of *G. maculata* from North Pare Mts, Lembeni the chromosomal number was reduced to  $2n = 27$ ; one medium pair was metacentric (FN = 29), whereas in second one probably acrocentric (not shown). One male of *G. immaculata* had mosaic cells with 29 and 27 chromosomes. C-banding revealed some differences in number and distribution of constitutive heterochromatin blocks (C-bands) between and within species (Fig. 22).

The study of spermatogonial, oogonial and somatic gastric caeca mitotic metaphase of *G. helleri* sp. n. showed in most cells 7 chromosomes, FN = 10, 11 in the male (Fig. 22D, F, G) and 8, FN = 11, 12 in the female (Fig. 22E). In all individuals the first long pair was meta/submetacentric, whereas the second long pair was polymorphic and characterized by three main karyomorphs (A, B, C) in respect to the morphology of homologous chromosomes and heterochromatin patterns of C-bands among analyzed specimens: (A) eight samples from the Udzungwa Mts and four from the Eastern Arc Mountains (Nilo forest reserve) presented meta- or submetacentric chromosomes in a homozygous or heterozygous state (Fig. 22D, E); (B) five individuals from the Udzungwa Mts and two coming from the Uluguru Mountains showed meta/submetacentric and acrocentric chromosomes (Fig. 22F); (C) one single male collected in the Uluguru Mts had homologous acrocentric chromosomes (Fig. 22G). After C-staining, chromosomes of this pair and in the third acrocentric pair showed quantitative variation in heterochromatin blocks among the analyzed individuals.



**Fig 22.** C-banded mitotic metaphase of male complement of *G. maculata* (A), female *G. immaculata* (B), male *G. furcata* sp. n. (C) as well as both male (D, F, G) and female (E) of *G. helleri* sp. n. Arrows indicate biarmed chromosomes in *G. furcata* sp. n. (C). In *G. helleri* sp. n. the long polymorphic pair 2 shows three main karyomorphs in which homologous chromosomes differ in their morphology: both meta- or submetacentric (D, E), meta/submetacentric : acrocentric (F) and both acrocentric (G). X, sex chromosome. Scale bar = 10 µm.

## Discussion

### Taxonomy

Four species of *Gonatoxidea* are known at present. However, further specimens stored in the entomological collection of the Natural History Museum in Vienna probably belong to new species of *Gonatoxidea*. One male is labelled “Zanzibar”, collected by A. Horn, showing cerci with only single sclerotized dents at their tips and an unlobed subgenital plate with short styli. Until further material gets available we decided not to describe this new species.

Another male specimen identified as “*Arantia spinulosa*” collected by A. Horn also belongs to *Gonatoxidea*. This specimen is labelled “MKaffa”, could thus come from Ethiopia. It is larger than *G. maculata* which it resembles in terms of male cerci, tegmina shape and maculation (Fig. 23). Since the locality is not clear further specimens have to be collected to clarify where this specimen is coming from and whether it belongs to a new species of *Gonatoxidea*.

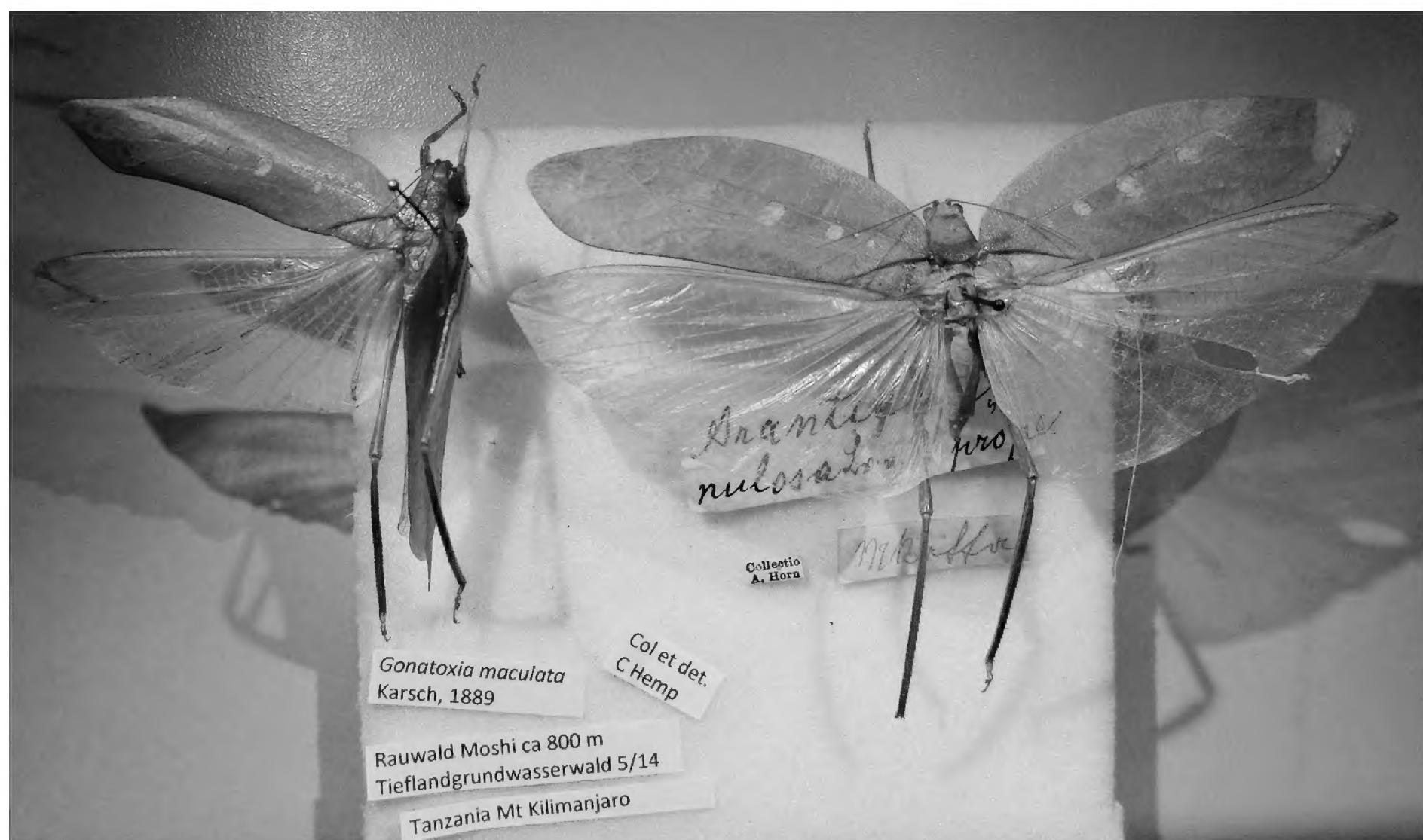
Further two specimens in Vienna were also studied, collected by Reimer labelled “DO Afrika” thus coming from Tanzania. Since the exact locality is unclear and the cerci could not be studied in detail without damaging the very old specimens a diagnosis to which species they belong is uncertain. One of the two males, however, could belong to *G. immaculata* since the subgenital plate agrees with males collected from the East Usambara Mountains and Kazimzumbwi Forest Reserve, the other to *G. maculata*. For the distribution of *Gonatoxidea* species in East Africa see Fig. 24.

Studying a larger series of *Gonatoxidea* specimens newly collected in Tanzania and from the entomological collections of Vienna and London showed that *Gonatoxidea* is a very uniform genus and well separated from *Dapanera* which it superficially resembles. However, molecular studies on *Dapanera* and *Gonatoxidea* are necessary to deepen our understanding about generic relationships, also on tribal level within Holochlorini.

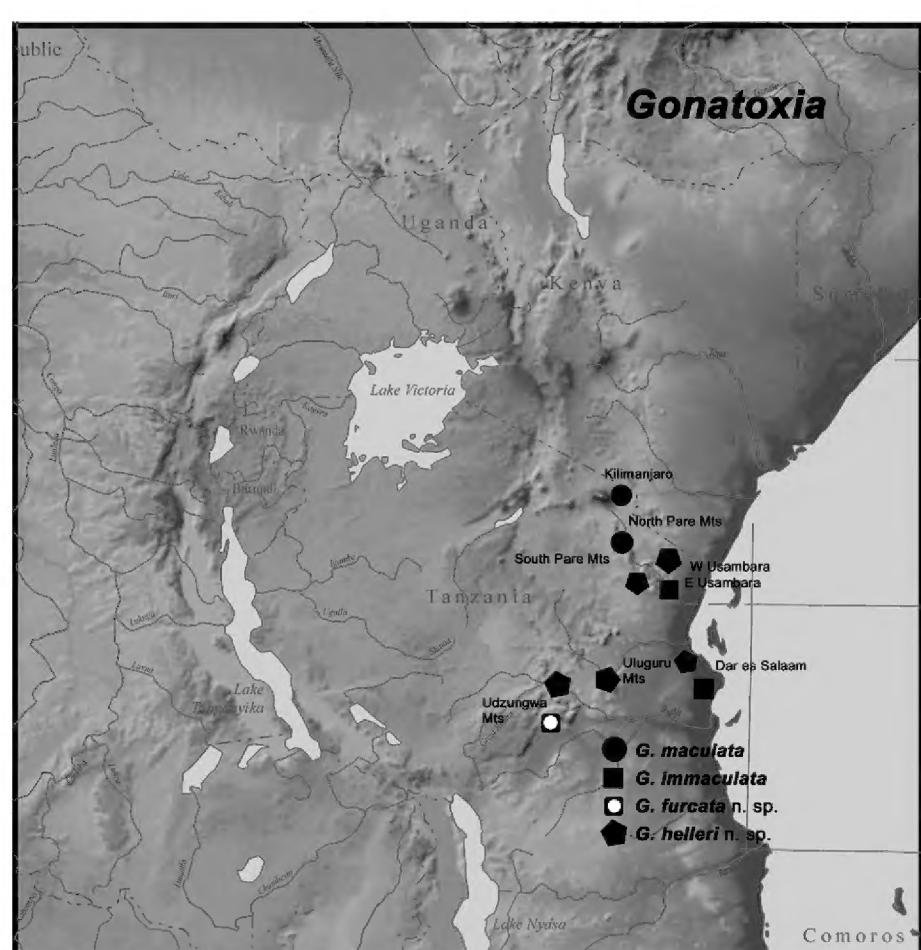
### Bioacoustics

The calling song of all four species of *Gonatoxidea* consists of very short, cricket-like, resonant syllables, separated by large silent intervals, similar as in the genus *Parapryrrhicia* Brunner von Wattenwyl (Hemp et al. 2016). The duty cycle (percentage of time with actual sound emission) of these songs is obviously very low, and singing males are certainly difficult to detect by acoustically orienting predators or parasitoids (for a more detailed discussion of the advantages of this song type see Hemp et al. 2016).

However, the structure of the stridulatory file of *Gonatoxidea* differs somewhat from that of *Parapryrrhicia*. The distribution of the inter-tooth intervals is similar, but from the anal end onwards the file runs on a slightly elevated bulge and the teeth are larger. In the larger teeth it is



**Figure 23.** Comparison of *G. maculata* male from Mt Kilimanjaro with specimen in the collection of Vienna labeled *Arantia spinulosa*.



**Figure 24.** Map of East Africa with distribution of *Gonatoxia* species. *G. maculata* in Somalia is not indicated since locality information is insufficient.

clearly visible that the steep side of the asymmetric teeth are directed to the anal side (Fig. 18). This structure has been observed only in species in which the sound is produced during the closing movement of the tegmina as in most tettigonioids (Heller 1988). According to a hypothesis of Montealegre-Z. (2012) decreasing tooth intervals from anal to basal - as found in *Gonatoxia maculata*, *G.*

*immaculata*, *G. furcata* and the anal part of *G. helleri* - could indicate that sound is produced during the opening of the wings (called 'reversed' stridulation). However, the structure of the teeth strongly suggests a 'normal' sound production and questions the usability of inter-tooth intervals for documenting 'reversed' stridulation.

### Chromosomes and evolution

The four species examined in this study revealed a remarkable variability in chromosome numbers and morphology. Patterns of chromosome evolution in this genus are very interesting and differ from the ancestral/model karyotype ( $2n = 31$  in the male with acrocentric chromosomes) found in most tettigoniids (e.g. Warchałowska-Śliwa 1998) and most other African Phaneropterinae genera, e.g. *Altihoratosphaga*, *Horatosphaga*, *Monticolaria*, *Lunidia*, *Parapryrrhicia* or *Tropidonotacris* (Hemp et al. 2010a, b; 2014; 2016). The ancestral chromosome number is reduced to  $2n = 29$  in *G. maculata* and *G. immaculata*, similar to *Eurycorypha* species (five species investigated so far; Hemp et al. 2013c) and *Plangia* (Hemp et al. 2015). This reduced chromosome number probably is the result of one tandem fusion. In *G. furcata* sp. n. the chromosome set is reduced to  $2n = 27$  ( $FN = 29$ ) probably by Robertsonian translocation, whereas an unexpected karyotype with only 7 chromosomes (in males) was revealed for *G. helleri* sp. n. Up to now such an exceptionally low chromosome number was not found in any tettigoniid species. Typical for the karyotype and also for the different karyomorphs of this species are very large autosomes compared to all other species of this genus, obviously caused by multiple rear-

rangements. Such significant differences in chromosome numbers and the morphology very likely resulted from successive tandem and Robertsonian fusions in various combinations. Our cytotoxic studies indicate that dramatic chromosomal rearrangements took place during speciation of *G. helleri* sp. n. which is one of the most wide-spread species of the genus so far. Detailed karyotype analyses of *Gonatoxia*, especially for *G. helleri* sp. n. using classic and molecular cytogenetics methods will be given by Warchałowska-Śliwa et al. (in prep).

## Conservation and bioindication

*Gonatoxia* species were rarely collected, partly because they are nocturnal species, well camouflaged in the tree layer of forests and seasonal. But they are rarely collected partly also because they occur in habitats that are vanishing rapidly and also never had a large extension formerly. *Gonatoxia maculata* was only caught in deciduous dry forests and a vegetation type which was called “Obstgartensteppe” = orchard steppe by the Germans, since the trees are scattered and resemble superficially fruit trees planted in an orchard. Both vegetation types are rapidly vanishing in East Africa. The North and South Pare Mountains for example still harbour deciduous dry forests especially at their northern slopes. However, a rapidly increasing human population impact these forests by cutting, burning and using also steepest slopes as range land for life stock these days. The same holds true for the vegetation type “Obstgartensteppe” which is almost lost e.g. on Mt Kilimanjaro. Thus the presence of species such as *Gonatoxia maculata* serve as information about the vegetation types they are bound to, and therefore this species can be used as a bioindicator. The same was suggested for *Tropidonotacris grandis* occurring in same habitat types as *G. maculata* (Hemp et al. 2014). Another type of habitat rich in biodiversity and endemics, lowland wet forest, is indicated by *Gonatoxia immaculata*, *G. furcata* sp. n. and *G. helleri* sp. n. Coastal and lowland forests, once a contiguous belt along the Kenyan and Tanzanian coasts and at the foothills of mountain ranges and mountains are almost entirely cleared away today. Only few patches, mostly protected as forest reserves, are left. With them an unique flora and fauna disappear replaced by scrub and grassland harbouring some wide-spread species at the most. Thus passing e.g. between Segera at the northern coastal strip to Chalinze near Dar es Salaam in Tanzania forest has been completely cleared away over hundreds of square kilometers and barren land supports meagerly brittle life stock today. Reforestation programmes for the production of timber and fire wood could take away the pressure from the remaining few patches of coastal and lowland forest and should urgently be initiated.

Species such as *Gonatoxia*, *Parapyrrhicia* and *Tropidonotacris* may be used as bioindicators allowing to follow land cover changes over time since early collections reach back as far as the 18<sup>th</sup> century. Thus the evaluation

of old collections are precious archives providing multiple data to e.g. model scenarios of how land cover changed over time and to identify areas which once harboured habitats rich in biodiversity, e.g. for restauration programmes. Thus even few specimens of certain species as shown above for the Vienna collection holding a couple of specimens of different *Gonatoxia* species provides insight of the vegetation covering the area more than 100 years ago.

## Acknowledgements

Part of this research received support from the Synthesis Project (<http://www.synthesys.info/>) financed by the European Community Research Infrastructure Action under the FP6 “Structuring the European Research Area Programme”, enabling us to visit collections in London, Vienna and Copenhagen. We gratefully acknowledge grants by the Deutsche Forschungsgemeinschaft and the Tanzanian Commission for Science and Technology (COSTECH) as well as the Tanzania Wildlife Research Institute (TAWIRI) for permitting research. Many thanks to Susanne Randolph, Sigfrid Ingrisch and Bruno Massa for improving the manuscript.

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